

A REVIEW OF THE TROPHIC ROLE OF MESOPELAGIC FISH OF THE FAMILY MYCTOPHIDAE IN THE SOUTHERN OCEAN ECOSYSTEM

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Abstract

Results of research into the trophic relationships of myctophids demonstrate that this group of mesopelagic fish plays a significant role in the community of Southern Ocean marine organisms. Myctophids have the trophic status of zooplankton consumers. The large amount of meso- and macroplankton consumed by myctophids indicates high abundance and biomass of these fishes. According to a preliminary estimate, the yearly consumption of zooplankton by *Electrona carlsbergi* ranges from 157 to 364 million tonnes. Myctophids occupy the third level in the Southern Ocean trophic system and are consumers of the second order. Myctophids play a major role as producers, supporting the production of organisms higher up the food chain (certain species of squid, notothenioids, seabirds and mammals).

Résumé

Les recherches sur les relations trophiques des Myctophidae indiquent que ce groupe de poissons mésopélagiques joue un rôle significatif dans la communauté d'organismes marins de l'océan Austral. Dans le réseau trophique, les Myctophidae ont le statut de consommateurs de zooplancton. La quantité importante de méso- et macroplancton consommée par les Myctophidae met en évidence le niveau élevé d'abondance et de biomasse de ces poissons. Selon une première estimation, la consommation annuelle de zooplancton par *Electrona carlsbergi* varie de 157 à 364 millions de tonnes. Les Myctophidae, consommateurs du deuxième ordre, occupent le troisième niveau du système trophique de l'océan Austral. Ils jouent un rôle important en ce qu'ils participent à la production d'organismes supérieurs dans le réseau trophique (certaines espèces de calmars, de Notothenioidei, d'oiseaux de mer et de mammifères).

Резюме

Результаты исследований трофических взаимоотношений миктофид показали, что данная группа мезопелагических рыб играет важную роль в сообществе морских организмов Южного океана. В трофической иерархии миктофиды имеют статус консументов зоопланктона. Большое количество мезо- и макропланктона в рационе миктофид указывает на высокую численность и биомассу этих рыб. Согласно предварительной оценке, годовое выедание зоопланктона рыбами вида *Electrona carlsbergi* составляет от 157 до 364 миллионов тонн. Миктофиды занимают третий уровень трофической системы Южного океана и являются консументами второго порядка. Миктофиды играют основную роль продуцентов и поддерживают продукцию организмов высших звеньев пищевой цепи (определенных видов кальмара, нототениевых, морских птиц и млекопитающих).

Resumen

Los resultados de los estudios sobre las relaciones tróficas de los mictófidos demuestran que este grupo de peces mesopelágicos desempeña una importante función en la comunidad de los organismos marinos del océano Austral. Los mictófidos se sitúan en la cadena alimentaria a nivel de consumidores de zooplancton. La gran cantidad de mesoplankton y macroplancton consumido por los mictófidos es indicativa de una gran abundancia y biomasa de estos peces. De acuerdo a un cálculo preliminar, el consumo anual de zooplancton por parte de *Electrona carlsbergi* varía de 157 a 364 millones de toneladas. Los mictófidos ocupan el tercer nivel en la cadena alimentaria del océano

Austral y son consumidores de segundo orden. Los mictófidos son productores importantes, ayudando en la producción de organismos a mas alto nivel en la cadena alimentaria (algunas especies de calamares, nototénidos, aves y mamíferos marinos).

Keywords: myctophids, mesopelagic trophic system, trophic relationships trophic levels, CCAMLR

INTRODUCTION

The ichthyofauna of the mesopelagic zone of the Southern Ocean is mainly composed of the families Myctophidae and Gonostomatidae. Myctophids dominate in terms of the number of species, their widespread distribution and the abundance of various species. There are more than 35 myctophid species in this area, 11 of which have a circumpolar distribution (Hulley, 1990).

It has been established that in Antarctic and sub-Antarctic waters myctophids are found mostly within the Antarctic Circumpolar Current (ACC), although their range also includes the Circumpolar Deep Water (CDW) (Lubimova *et al.*, 1987). The region of highest myctophid abundance, however, is the Polar Frontal Zone (PFZ), where high plankton productivity provides the feeding grounds for myctophids. Mean yearly production of zooplankton in this area is 1.2 billion tonnes (Voronina *et al.*, 1980; Lubimova *et al.*, 1987). Inhabiting the ACC, myctophids are capable of reaching fairly high latitudes (62° to 65°S; sometimes even further south) where ACC waters extend southward.

Years of research undertaken by VNIRO (All-Russia Research Institute of Marine Fisheries and Oceanography), Sevrybpromravvedka (North Fishery Survey Board) and various other institutions in Russia have produced a large volume of data which is currently assisting not only in determining the main ecological characteristics of myctophids, but also in identifying those abundant species which are capable of forming dense concentrations. Such species include: *Electrona carlsbergi*, *Electrona antarctica*, *Gymnoscopelus nicholsi*, *Krefftichthys anderssoni* (Lubimova *et al.*, 1987).

The primary objective of this study is to determine the position of mesopelagic fish in the trophic structure of the Southern Ocean, as well as to identify and quantify the dietary relationships between these mesopelagic species and organisms above and below them in the food chain.

This study is mainly based on published and unpublished results of research undertaken by VNIRO and other national research institutes. Published results of studies carried out by scientists of other countries are also used in discussions.

RESULTS AND DISCUSSION

Myctophids are part of the mesopelagic trophic system (Parin, 1971) and are large-scale consumers of meso- and macroplankton, primarily copepods, amphipods and euphausiids.

Both the availability of zooplankton to mesopelagic fishes (mainly the abundant myctophid species) in oceanic Antarctic waters and the stability of the food supply at various stages of these fishes' development are adequate because the waters of the PFZ are characterised by high concentrations of zooplankton not only during the summer peak, but throughout the entire year, and by high plankton productivity to depths of 500 m or greater (Voronina, 1971 and 1977).

Seasonal vertical migration is typical of Antarctic zooplankton. In the summer, zooplankton occurs in the surface water layers, descending to greater depths in the winter. This plankton distribution is linked to the seasonal vertical migrations of its main consumers, including mesopelagic fish, particularly myctophids. In the spring and summer seasons (November to March), myctophids ascend to the epipelagic zone (50 to 200 m) and feed in the stratum of high summer plankton productivity. In the winter, they descend to greater depths (350 to 500 m) and inhabit the top layer of CDW which contains the wintering populations of planktonic crustaceans (Lubimova *et al.*, 1983 and 1987).

The following abundant copepods are the dominant plankton species: *Calanus propinquus*, *Calanus simillimus*, *Calanoides acutus*, *Rhincalanus gigas* and *Metridia gerlachei* (Voronina, 1971 and 1977). These species are the main prey items of myctophids. Apart from copepods, the following are also important in the myctophid diet:

Hyperiidae (particularly *Parathemisto gaudichaudii*) and Euphausiacea (mainly *Euphausia superba* and *Thysanoessa macrura*) (Kozlov and Tarverdieva, 1989; Kozlov and Shust, 1991; Rembiszewski *et al.*, 1978; Rowedder, 1979). Planktonic crustaceans form the main food supply of myctophids inhabiting open Antarctic waters. Chaetognatha and Pteropoda also frequently occur in the diet of myctophids.

Research into the myctophid diet showed that food type varies according to habitat. In the PFZ, sub-Antarctic regions and high-latitude waters, the main components of the diet are, respectively, copepods, hyperiid amphipods and euphausiids (Lubimova *et al.*, 1983; Tarverdieva, 1986). In high-latitude areas, however, feeding by myctophids on euphausiids is limited because the depth distribution of the former (greater than 200 m) is below the depth of krill concentrations. The diversity of species and groups of prey organisms found in the stomachs of myctophids indicates that they feed on the most abundant available plankton. Differences observed in the diets of myctophids from various areas are mainly determined by regional and seasonal variability in zooplankton composition.

Quantitative data on the dietary requirements of myctophids are vital for assessing the role of these fishes in the Antarctic ecosystem. Detailed studies are rare, however, and all deal only with the most abundant species in the PFZ; *E. carlsbergi*. In particular, papers by Naumov *et al.* (1981) and Kozlov and Shust (1991) put forward the assumption that in the summer season (from December to February) the daily dietary intake for this species in the Scotia Sea and the PFZ is close to the value for the overall rate of consumption, which amounts to 3.27% and 3.86% of body weight respectively. A similar rate of consumption, 3%, was recorded for the highly abundant species from the tropical part of the Pacific Ocean, *Myctophum nitidulum* (Tseitlin and Gorelova, 1978).

Daily consumption by *E. carlsbergi* in the PFZ was calculated using data from other investigations of changes in the index of stomach fullness over a 24-hour period. In the summer (February), daily consumption varied between 3.7 and 5.6% of body weight (Gerasimova, 1990), whereas in autumn (March) it amounted to 1.4% of body weight (Podrazhanskaya and Tarverdieva, 1991). Using data on mean annual growth and metabolic rate, the annual food intake of *E. carlsbergi* was calculated at 15 times its body

weight with a daily intake of 4% body weight (Gerasimova, 1990). In our opinion the annual value is overestimated. Studies on the diet of *E. carlsbergi* carried out during different seasons showed that in the winter and spring periods feeding intensity is only half to one-third of the summer levels (Kozlov and Shust, 1991). Allowing for the possibility that the preliminary studies have overestimated zooplankton consumption by *E. carlsbergi*, annual consumption is taken to be half the original estimate, i.e. from seven to eight times body weight.

Myctophid biomass in the Southern Ocean has been estimated to be 70 to 130 million tonnes (Lubimova *et al.*, 1987). On the basis of the proportions of the most abundant myctophid species in catches of pelagic trawls, it appears that 80% of the biomass comprises the four species *E. carlsbergi*, *E. antarctica*, *K. anderssoni* and *G. nicholsi*. Results of biomass assessments of *E. carlsbergi* carried out in recent years in the PFZ for all three ocean basins shows that the biomass of this species may account for between 40 and 50% of the total biomass of these four species, i.e. from 22.4 to 52 million tonnes. In this case, the annual consumption of zooplankton by *E. carlsbergi* (based on a consumption rate of seven times body weight per annum) can be estimated at 157 to 364 million tonnes.

The impact of predators on myctophid populations in the Southern Ocean ecosystem is not well understood. At the same time, it is known that myctophids are a food source for organisms higher up the food chain in shelf areas, the continental slope and the open ocean.

An analysis and summary of data from more than 50 publications (from 1984 onwards) by Sabourenkov (1991) produced an assessment of the role of myctophids in the diet of Antarctic predators. A large number of publications concerned variation in diets between species in higher taxonomic groups, e.g. fish, squid, marine birds and mammals. Myctophids were found in the diets of one species of squid, 18 species of fish (Nototheniidae - 8, Channichthyidae - 7, Bathyraconidae - 2, Rajidae - 1), 18 species of marine bird (penguins - 7, albatrosses - 4, petrels - 5, prions - 1, cormorants - 1) and two species of seal (elephant and southern fur seal). The published data demonstrate that myctophids are of secondary importance in the diets of many predator groups. However, they are the primary food source for only some marine birds, e.g. the king penguin.

Although existing publications contain a great deal of material, they do not give a full account of the trophic relationships of predators. It should be pointed out that at present there are insufficient data to calculate the consumption of myctophids by the various predator groups. It is therefore vital to study the quantitative relationships between myctophids and their predators, which ultimately control the dynamics of the predator and prey populations. At the same time, considering the current state of knowledge, it should be possible to develop new approaches to the quantitative assessment of predator consumption (daily, yearly). A good example of this is the development of a model to evaluate food consumption by marine birds (Croxall *et al.*, 1990). This paper on the feeding habits of seabirds in the South Georgia area estimates annual myctophid consumption at about 240 000 tonnes. Our own material on the feeding of squid and fish will supplement the summary analysis carried out by Sabourenkov (1991) (see Table 1).

Squid

Research into the feeding habits of the abundant mesopelagic squid species *Mesonychoteuthis hamiltoni*, *Moroteuthis knipovitchi* and *Martialia hyadesi* shows that mesopelagic fish, mainly myctophids, comprise the bulk of these squids' diet (Klumov and Yukhov, 1975; Naumov, 1985; Nemoto *et al.*, 1984; Rodhouse *et al.*, 1992). Data from the thirteenth cruise of the vessel *Vozrozhdenie* in the Falkland/Patagonian area (46°00' to 46°30'S, 58°30' to 60°00'S) show that the highly abundant squid species *Illex argentinus* feeds mainly on myctophids (frequency of occurrence - 95 to 100%). The diet of the mesopelagic squid *M. hamiltoni* included myctophids *E. antarctica* and *Gymnoscopelus braueri* (Klumov and Yukhov, 1975).

According to calculations carried out by Naumov (1985), the total annual consumption of food by *M. hamiltoni* is 120 million tonnes.

Table 1: Myctophids in the diet of several species of squid and fish in various areas of the Southern Ocean.

Myctophid Species	Consumers	Dietary Role	Area	Reference
<i>Myctophidae</i> sp.	Squid: <i>M. hamiltoni</i>	****	Open waters	Klumov and Yukhov, 1975
<i>G. braueri</i> <i>E. antarctica</i> <i>Myctophidae</i> sp.	<i>I. argentinus</i>	***	Patagonian area	Unpublished data (VNIRO)
<i>Gymnoscopelus</i> sp.	Fish: Nototheniidae <i>N. rossii marmorata</i>	**	South Georgia	Unpublished data (VNIRO)
<i>E. Carlsbergi</i> <i>G. nicholsi</i>	<i>N. squamifrons</i> <i>D. eleginoides</i> (trawl catches)	** ** **	Shag Rocks South Georgia	
<i>Protomyctophum</i> sp. <i>Myctophidae</i> sp.	<i>D. eleginoides</i> (longline catches)	***	South Georgia	Konforkin and Kozlov, 1992
<i>Myctophidae</i> sp. <i>Electrona</i> sp. <i>Gymnoscopelus</i> sp. <i>Electrona</i> sp.	Trichiuridae: <i>P. antarcticus</i>	***	Scotia Sea South Georgia South Sandwich Is.	Podrazhanskaya and Pinskaya, 1987 Rembiszewskiet al., 1978
<i>Myctophidae</i> sp.	Macruridae: <i>C. holotrachus</i>	*	Patagonian area	Personal data
<i>Myctophidae</i> sp.	Scombridae: <i>T. thynnus</i>	**	Patagonian area	Personal data

**** main dietary component
*** regular component
** minor component
* occasional component

Considering that mesopelagic fish comprise up to 80% of the diet of this particular squid (Klumov and Yukhov, 1975) and that myctophids account for 50 to 60% of that amount, one may assume that yearly consumption of myctophids by *M. hamiltoni* is in the order of 48 to 57 million tonnes.

Fish

Information on the occurrence of myctophids in the diet of Antarctic fishes shows that their role in fish diets is not great, as they are generally of secondary importance as prey items (Sabourenkov, 1991). This is particularly true of species inhabiting island shelf waters. Over the continental slope at depths greater than 600 m (e.g., for Patagonian toothfish), the dietary significance of mesopelagic fish (Myctophidae and Gempylidae) increases (Konforkin and Kozlov, 1992). Myctophids dominate the diet of predatory mesopelagic fish, especially for the species *Paradiplospinus antarcticus* of the family Trichiuridae (Rembiszewski *et al.*, 1978; Podrazhanskaya and Pinskaya, 1987). Calculations of daily and yearly consumption, however, are given only in a few publications (Pakhomov and Tseitlin, 1991). It is therefore not yet possible to estimate the consumption of myctophids by predatory fish.

Birds

Myctophids are important in the diet of Antarctic penguins, especially in the vicinity of Antarctic and sub-Antarctic islands (Williams, 1988; Croxall *et al.*, 1990).

The role of flying seabirds as myctophid consumers is not altogether clear. Antarctic myctophid species do not normally form near-surface concentrations. As a result they are not very accessible to flying seabirds, which are unable to dive as deep as penguins. Furthermore, myctophid consumption by flying seabirds is usually estimated from analysis of otoliths in the birds' stomachs. According to Sabourenkov (1991), the presence of myctophid otoliths in the stomachs of these seabirds may indicate that these fishes are direct prey items or that they occur in the birds' stomachs via the diet of their primary prey, such as nototheniids and channichthyid fish or squid.

Mammals

Marine mammals, with the exception of fur seals, do not generally have very close trophic links with myctophids. Toothed whales, in particular the sperm whale, feed mainly on the squid *M. hamiltoni*, which is itself a consumer of mesopelagic fish, primarily myctophids (Klumov and Yukhov, 1975).

CONCLUSIONS

The results of research on the trophic relations of myctophids show that this group of mesopelagic fish plays a significant role in the Southern Ocean ecosystem. Firstly, they consume a large quantity of the abundant meso- and macroplankton and secondly, their resultant high biomass provides forage for organisms at higher trophic levels (squid, notothenioids, penguins and marine mammals). Myctophids have the trophic status of zooplankton consumers; they occupy the third level in the trophic system of the Southern Ocean and can be classified as second order consumers.

The trophic relationships summarised by Sabourenkov (1991) show that the food chain of marine organisms in Antarctic waters has five levels: a primary production level (phytoplankton) and four levels of consumers. Direct consumers of myctophids (squid, fish, penguins, southern fur seal) occupy the fourth trophic level, i.e. third order consumers.

Investigations of the general pattern of energy transfer between planktonic crustaceans and myctophids showed that primary productivity is transformed into fish production mainly via a relatively small number of intermediate predatory species. Therefore the linkage is short and direct: phytoplankton - mesoplankton - myctophids.

It is known that effective energy transfer depends upon the degree of consumption of organisms of lower trophic levels by consumers higher up the food chain. In Antarctic waters, the end product mainly comprises primary predators, i.e. fish such as lanternfish and many notothenioid species feeding on herbivorous planktonic crustaceans (copepods and euphausiids). Some myctophids such as *E. carlsbergi*, *E. antarctica*, *K. anderssoni* and *G. nicholsi* attain high abundance and biomass (Lubimova *et al.*, 1987).

We do not have accurate data on the abundance of consumers of a high trophic level, e.g., the deepwater Antarctic squid *M. hamiltoni* and some species of penguin, which are the main predators of myctophids. Nevertheless there is evidence of a high biomass of *M. hamiltoni* in the order of 60 million tonnes, based on estimates of the daily consumption of sperm whales and numbers of squid beaks found in whales' stomachs (Klumov and Yukhov, 1975).

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Liste des tableaux

Tableau 1: Myctophidae dans le régime alimentaire de plusieurs espèces de calmars et de poissons en divers secteurs de l'océan Austral.

Список таблиц

Таблица 1: Миктофиды в рационе ряда видов кальмара и рыбы в различных районах Южного океана.

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Tabla 1: Mictófidos en la dieta de varias especies de calamares y peces en diversas zonas del océano Austral.

